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Independent Development of Bilaterally Homologous Closer Muscles in Lobster Claws

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Abstract. The fiber composition of the closer muscle in the paired claws of the lobster *Homarus americanus* was determined in juvenile 8th and 9th stage animals following various experimental manipulations of the substrate and the claws in the early juvenile 4th and 5th stages. One of the paired muscles developed 90% fast fibers and 10% slow fibers, typical of a cutter claw. The other muscle varied in its fiber composition with fast fibers ranging from 10–90%. This range was categorized into three muscle types: a cutter with 70–90% fast fibers, a crusher with 10–30% fast, and an intermediate with 40–60% fast. The paired homologous claw closer muscles therefore develop such that one is preprogrammed as a cutter while the other is more plastic and develops along a gradient ranging from a cutter to a crusher.

Introduction

One of the puzzling aspects in the development of animals with bilateral symmetry is the appearance of asymmetry in homologous structures. An excellent example of such bilateral asymmetry is found in the enlarged chelipeds or claws of crustaceans such as male fiddler crabs, hermit crabs, snapping shrimps, and lobsters. In these, the paired claws consist of a major and a minor type. In the lobster, *Homarus americanus*, the asymmetry is expressed not only in the external morphology but in the fiber composition of the closer muscle as well (reviewed by Govind, 1984). Thus the major or crusher claw has a closer muscle comprised entirely of slow fibers; the minor or cutter muscle has predominantly fast fibers. Moreover, claw laterality is random (Herrick, 1911) and is determined during the juvenile 4th and 5th stages when the paired claws and closer muscles are still bilaterally symmetric (Emmel, 1908; Lang *et al.*, 1978). Once claw type is determined during the critical period, it is fixed for life (Emmel, 1908). The determination of claw type appears to initially involve the CNS and only later involves changes in the claw itself (Govind and Pearce, 1986). One of these changes is in the fiber composition of the closer muscle which may be bilaterally symmetric or asymmetric. By examining a large number of paired muscles in both configurations, we deduce that these bilaterally homologous muscles develop independently of each other. One of the paired muscles invariably develops as a cutter; the other muscle develops along a gradient ranging from a cutter to a crusher.

Materials and Methods

Larval lobsters (*Homarus americanus*) were obtained from the Massachusetts State Lobster Hatchery on Martha's Vineyard. They were reared at the Marine Biological Laboratory by procedures described previously (Lang, 1975) until the 8th or 9th stage, a period of three to four months from June to September. The molt history of each lobster and of its paired claws was recorded. Muscle fiber typing was performed histochemically by staining for myofibrillar ATPase activity via standard procedures (Ogonowski *et al.*, 1980). Cross-sections in the mid region of the claw, where the closer muscle had the largest area, were photographed and printed with a final enlargement of 100×. The percentage of fast and slow muscle fibers was calculated from these photographic prints by one of two methods, each of which yielded results varying by 2%. Thus the cross-sectional surface area occupied by each fiber type was calculated via (i.) a transparent acetate overlay marked in centimeter squares or (ii.) weighing "cut-outs" of the relevant areas.

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The lobsters reported in this study came from a series of experiments in which the 4th and 5th stage were treated in various ways to control claw laterality. These treatments are classified under one of the following categories: (i.) no substrate in the 4th and 5th stages; (ii.) oyster chips provided at selected intervals during the 4th and 5th stages; (iii.) oyster chips provided in the 4th and 5th stages but with one of the claws immobilized by glueing it shut; or (iv.) oyster chips in the 4th and 5th stages but with one of the claws removed. All of these treatments, except the first, induced the development of paired asymmetric, cutter and crusher claws in the majority of lobsters (Govind and Kent, 1982). The first treatment suppressed the development of a crusher claw in a majority of lobsters, and instead produced lobsters with paired cutter claws. The present report quantitatively examines the fiber composition of the paired closer muscles from representative examples of lobsters reared under a variety of conditions. In this way the variability between bilaterally homologous muscles may be documented and developmental interactions between them noted.

Results and Discussion

The determination of claw type was usually made in the juvenile 8th or 9th stage on the basis of external morphology. At this stage the crusher appeared as a slightly stouter claw with a central molar-like tooth compared to the cutter which is a more slender claw and has a central incisor-like tooth (Herrick, 1911; Emmel, 1908). Occasionally, a claw appeared that was difficult to characterize as either a crusher or cutter since it had an external morphology intermediate to the two types. This unusual intermediate type as well as the usual cutter and crusher type claws were studied for the fiber composition of their closer muscles. However, in all cases the muscles were examined in bilaterally paired claws which included the asymmetric configuration of a cutter claw and either a crusher or an intermediate claw, and the symmetric configuration of paired cutter claws. Representative examples of the closer muscles from these three configurations of paired claws are shown in Figure 1. The percent composition of fast and slow fibers from the paired closer muscles of 35 animals is listed in Table 1. The listing showed that one of the paired muscles was invariably a cutter type with a fairly constant composition of 90% fast and 10% slow fibers. The distribution of these fiber types was also constant; the fast muscle occupied most of the cross-sectional area while the slow muscle was restricted to a narrow ventral band (Fig. 1). The other claw of the homologous pair had a fast fiber composition ranging from 10 to 90%. In other words, the contralateral muscle was either another cutter muscle with 70–90% fast fibers, a crusher muscle with 10–30% fast, or an intermediate muscle with 50% fast.

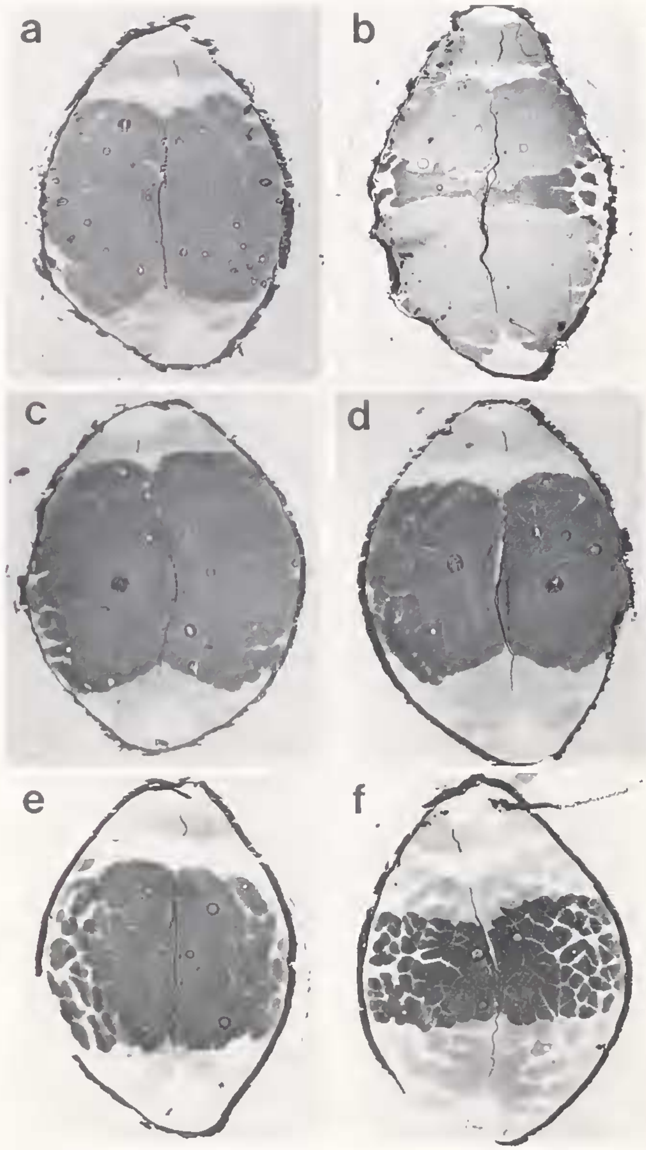

Figure 1. Representative cross-sections of bilaterally paired claws in juvenile 8th stage lobsters. In each section, the small, dorsally situated opener muscle stains lightly for myofibrillar ATPase activity, indicating slow fibers. The massive closer muscle has a mixture of light and dark staining indicating slow and fast fibers, respectively, which are classified into three types: a cutter type (a, c, d, e) with a majority of fast fibers, a crusher type (b) with a minority of fast fibers, and an intermediate type (f) with equivalent fast and slow fiber populations. The paired muscles therefore represent an asymmetric (a, b), symmetric (c, d), and intermediate (e, f) configuration in which one of the muscles is a cutter type (a, c, e) and the other is a crusher (b), another cutter (d), or an intermediate (f). Magnification = 25×.

The relationship between paired homologous muscles is better seen when the fiber composition of one muscle is plotted against that of its counterpart (Fig. 2); in this case the fast fiber composition was used. It became even more apparent that one of the paired muscles, either the

Table I

Muscle fiber composition of paired homologous claw closer muscles among juvenile 8th and 9th stage lobsters following various treatments in the 4th and 5th stages

		Muscle 1		Muscle 2	
Treatment	Stage	% Fast	% Slow	% Fast	% Slow
No substrate in 4th, 5th:	8	90	10	47	53
	8	90	10	85	15
	8	90	10	51	49
	8	90	10	30	70
	9	90	10	78	22
	9	93	7	50	50
	9	90	10	16	84
	9	90	10	72	28
	9	90	10	90	10
	9	90	10	26	74
	9	93	7	80	20
	9	90	10	90	10
Substrate:					
in 4th	8	90	10	10	90
	8	90	10	50	50
	8	90	10	50	50
	8	85	15	48	52
in 5th	8	90	10	13	87
	8	90	10	90	10
	8	90	10	85	15
in early 5th	8	90	10	10	90
	8	93	7	15	85
	8	90	10	43	57
	8	83	17	83	17
in 4th, and 5th	9	90	10	90	10
	9	90	10	13	87
Substrate and one claw immobilized	8	91	9	48	52
	8	90	10	10	90
	8	90	10	50	50
	8	90	10	75	25
Substrate and one claw removed	8	90	10	45	55
	8	90	10	15	85
	8	90	10	40	60
	9	90	10	27	73
	9	90	10	56	64
	9	90	10	25	75

right or left one, was invariably of the cutter type with 90% fast fibers. The other muscle had a fast fiber population typical of a cutter, crusher, or intermediate type and therefore developed independently of its homologous counterpart.

How may such independent development of bilaterally homologous muscles occur? To formulate an hypothesis regarding this question, recognizing certain salient features about the development of paired homologous muscles is helpful. First, these lobsters did not develop paired crusher claws; nor has there been a single case of such a symmetrical configuration recorded in over 2000 laboratory-reared lobsters in the past 15 years in our facilities at the Marine Biological Laboratory. However, lobsters with paired crusher claws are occasionally found in the wild (Herrick, 1911) but even in these one of the paired closer muscles had approximately 40% fast fibers (Govind and Lang, 1979). Second, and as a corollary to the first point, is the fact that one of the paired claws invariably developed into a cutter. Third, not only did one claw become a cutter, but its closer muscle had almost a fixed fiber composition of 90% fast and 10% slow. In other words, the development of one of the paired muscles appeared to be a preprogrammed event. Fourth, the other (contralateral) muscle of a pair showed variability in its fiber composition. The variability was seen not only in that this second muscle became either a crusher, intermediate, or cutter type, but also in the fact that even as a cutter muscle its fast fiber composition ranged from 70–90% as compared to the almost fixed value of 90% for the preprogrammed cutter muscle. In this respect the second muscle of the homologous pair showed developmental plasticity. Thus, there appeared to be a divergence in the expression of phenotype between the paired homologous muscles in that while one muscle acquired its fiber composition according to a

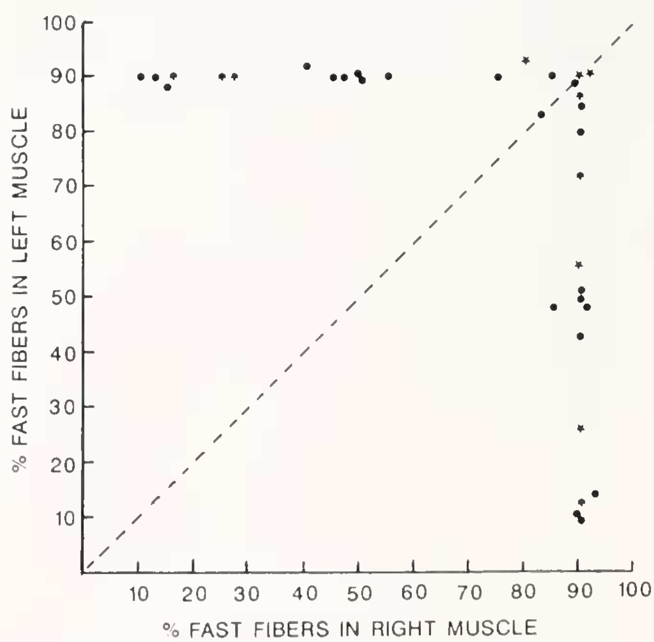

Figure 2. Relationship between the paired right and left closer muscles in terms of percent fast fibers in juvenile 8th (circles) and 9th (stars) stage lobsters. The broken line represents a line of symmetry where the paired muscles would be identical in fiber composition. The data points cluster about this line in the case of lobsters with paired cutter muscles but lie far from this line in the case of lobsters with paired cutter/crusher claws.

fixed program, its counterpart followed a more plastic route.

The initial decision for claw placement is made on the basis of differences in reflexive activity from the claws themselves (Govind and Pearce, 1986). Exercising one of the claws by making it reflexly grip an object causes that claw to develop into a crusher while the opposite claw becomes a cutter. However, when both claws were exercised neither became a crusher but both developed as cutters. These experiments suggest that neural input from the reflexively evoked claw activity impinging on the CNS, in this case the first thoracic ganglion, induces the side with the higher activity to become the crusher side while the opposite side becomes the cutter. When bilateral differences in neural input are minimal, the CNS fails to be lateralized and both sides develop into cutter types. Indeed, the cutter claw would represent a primitive type which would develop irrespective of any extrinsic influences such as reflexive claw activity. This would explain why when claw activity is minimized, such as when lobsters are reared without a substrate (Govind and Kent, 1982), both claws develop as cutters. For a crusher claw to develop, additional instructions must be superimposed onto the primitive cutter pattern—instructions which would promote the differentiation of slow fibers. These instructions would be restricted to one side as they arise because of bilateral differences. They would also have to be graded in nature to account for the fact that the second muscle may have a variable percentage of slow fibers.

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